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Pattern formation for reactive species undergoing anisotropic diffusion

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Abstract. Turing instabilities for a two species reaction-diffusion system is studied under anisotropic diffusion. More specifically, the diffusion constants which characterize the ability of the species to relocate in space are direction sensitive. Under this working hypothesis, the conditions for the onset of the instability are mathematically derived and numerically validated. Patterns which closely resemble those obtained in the classical context of isotropic diffusion, develop when the usual Turing condition is violated, along one of the two accessible directions of migration. Remarkably, the instability can also set in when the activator diffuses faster than the inhibitor, along the direction for which the usual Turing conditions are not matched.

1 Introduction

Spatio-temporal patterns are widespread in nature: beautiful spots and stripes appear on the coat of animals [1], patterns of cracking emerge on the fracture surface of materials [2], reacting chemicals give rise to complex and dynamical structures as in the celebrated Belousov-Zhabotinsky reaction [3–5], spatial games in social sciences yield self-organized regular motifs [6–9]. A common feature which is shared by the above mentioned applications is the spontaneous formation of complex structures, which result from the non trivial interplay between noise and deterministic dynamics. Elucidating the key mechanisms that seed the process of pattern formation is therefore an important topic of investigation of cross disciplinary impact.

One of such mechanisms was identified and thoroughly discussed in a pioneering work of Turing [10]: homogeneous equilibrium solutions of a multi-species reaction-diffusion system can be destabilized upon injection of a small inhomogeneous perturbation. This latter undergoes an exponential amplification, in the linear regime of the evolution. Then, nonlinearities come into play and the system eventually reaches a patchy, spatially inhomogeneous, equilibrium. Traveling waves and spiraling patterns can be also generated following a Turing-like, symmetry breaking instability.

In the classical setting, two mutually interacting species are considered: these are the so-called activator

and inhibitor. If the diffusion is isotropic, or in other words not affected by the specific direction of displacement, the inhibitor species should diffuse faster than the activator, for Turing patterns to develop. Systems of three simultaneously diffusing species [11] have also been considered in the literature and shown to display a richer zoology of possible instabilities and pattern. In this generalized context, self-organized motifs can also develop, if one species is solely allowed to diffuse in the embedding medium [12]. Beyond the deterministic scenario, stochastic Turing patterns have been also reported for reaction-diffusion systems defined on a regular lattice or complex networks [13–16].

Starting from these premises, and with reference to the paradigmatic scenario where just two species are made to interact, we shall here revisit the conditions that yield the Turing instability, under the assumption of anisotropic diffusion. More concretely, we shall derive sufficient conditions for the emergence of Turing like patterns in a rectangular, continuous, domain subject to periodic boundary conditions, assuming generic nonlinear reaction terms and imposing anisotropic, i.e. direction sensitive, diffusion coefficients.

As we will demonstrate in the following, patterns do exist also if the condition for the onset of the Turing instability is uniquely satisfied along one direction. These latter patterns resemble quite closely those that are found under the standard assumption of isotropic diffusion, the non-linearity being responsible for the mixing of cross modes. In addition, patterns can also flourish when the activator diffuses faster than the inhibitor, along one specific

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direction. In this case, the system organizes along the direction orthogonal to the latter, hence displaying regular, just locally distorted, stripes.

Since the pioneering work by Turing, the physico-chemical community largely studied the emergence of patterns, both theoretically and experimentally, highlighting different mechanisms that extend the theory beyond the standard instability paradigm. Whilst the inspected phenomena have distinct origins, similar models are often recovered, which require generalized schemes of diffusion, including anisotropic effects.

Chemical reactions occurring on substrates – solid catalysis – can for instance instigate patterns which appear to be modulated by the curvature of the hosting medium [17]. Adapted curvilinear coordinates can be introduced, thus yielding diffusion coefficients function of the space variables. In this case, the modified Laplace operator contains first order derivatives, acting as effective drift terms. Diffusion coefficients depending on the state variables can be obtained when e.g. modeling chemotaxis [18–22]. When linearizing the governing equations around the homogeneous equilibrium, one deals in fact with space dependent diffusion constants, which are however not sensitive to the specific direction of transport, at variance with the setting that we shall inspect hereafter¹. Similar considerations apply when studying generic gradient-like mechanisms of material transport [23,24].

Other models have been proposed which include cross diffusion terms [18,22,25–32]. Also in this case, the effective diffusion constants, obtained upon linearization, do not depend on the selected direction of transport.

In general Turing instability can develop once there is a differential in the species distribution. Researchers realized that these conditions are met for reactions occurring in liquid phases, once different species have distinct advection velocities. This phenomenon is termed *differential-flow-induced chemical instability* [33–35]. The linear stability analysis results in effective diffusion coefficients, depending on the mean velocity of one species and thus reflecting the specific direction of propagation. The imposed advection yields a first order operator which alters the prototypical structure of a reaction-diffusion scheme, as we shall here consider. The simplified framework that we propose could prove indeed useful to model reaction-diffusion processes in crystals [36], where the anisotropy is dictated by the geometry of the hosting medium.

The paper is organized as follows. In Section 2 we will present the reference framework and then, in Section 3 derive the mathematical conditions for the generalized anisotropic instability. Section 4 is devoted to reporting

some numerical tests to validate the theoretical analysis. Finally, we shall sum up and conclude.

2 Anisotropic diffusion of reactive species on continuum domains

Let us consider two interacting species and denote by u and v their respective concentrations. The species can freely diffuse inside a rectangular domain, $R = [0, L_x] \times [0, L_y] \subset \mathbb{R}_+ \times \mathbb{R}_+$, as specified by their respective diffusion coefficients. We shall in particular assume that the diffusion coefficients are anisotropic, meaning that they depend on the specific direction of migration. More precisely, $D_u^{(x)} \geq 0$ denotes the diffusion coefficient for species u along direction x , while $D_u^{(y)} \geq 0$ refers to the orthogonal direction y . Similar considerations respectively apply to $D_v^{(x)} \geq 0$ and $D_v^{(y)} \geq 0$. The mutual evolution of species u and v is thus governed by the reaction-diffusion equations:

$$\begin{cases} \dot{u} = f(u, v) + D_u^{(x)} \partial_x^2 u + D_u^{(y)} \partial_y^2 u \\ \dot{v} = g(u, v) + D_v^{(x)} \partial_x^2 v + D_v^{(y)} \partial_y^2 v \end{cases} \quad \forall (x, y) \in R \text{ and } \forall t > 0 \quad (1)$$

where $f(\cdot, \cdot)$ and $g(\cdot, \cdot)$ are nonlinear functions of the concentration amounts. The above equations should be complemented by the initial conditions:

$$u(x, y, 0) = u_0(x, y) \quad \text{and} \quad v(x, y, 0) = v_0(x, y) \quad \forall (x, y) \in R, \quad (2)$$

for some regular functions u_0 and v_0 , and suitable boundary conditions. In the following we shall adopt the Dirichlet periodic boundary conditions, namely

$$\begin{cases} u(x, 0, t) = u(x, L_y, t) \quad \forall x \in [0, L_x] \quad \text{and} \quad \forall t > 0 \\ u(0, y, t) = u(L_x, y, t) \quad \forall y \in [0, L_y] \quad \text{and} \quad \forall t > 0, \end{cases} \quad (3)$$

and similarly for v .

Let us assume the system (1) admits a stable, spatially homogeneous, solution $u = \hat{u}$ and $v = \hat{v}$. This request translates in:

$$\begin{cases} f(\hat{u}, \hat{v}) = 0 \\ g(\hat{u}, \hat{v}) = 0 \end{cases} \quad \text{such that: } \text{tr}(J) = f_u + g_v < 0 \text{ and} \\ \det(J) = f_u g_v - f_v g_u > 0 \quad (4)$$

where J stands for the Jacobian matrix of system (1):

$$J = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \quad (5)$$

where f_u denotes the derivative of $f(u, v)$ with respect to u , and similarly for f_v, g_u, g_v . Here, and throughout the remaining part of the paper, we evaluate the partial derivatives at the equilibrium point (\hat{u}, \hat{v}) . Without losing generality, we will also assume $f_u > 0$ and $g_v < 0$: u is

¹ The diffusive part of a generic model of state dependent diffusion can be written as $\nabla \cdot (D(u) \nabla u) = D'(u) \|\nabla u\|^2 + D(u) \Delta u$. Let assume u_0 be the homogeneous equilibrium and let us write $u = u_0 + \xi$ assuming ξ to be small, hence $D'(u) \|\nabla u\|^2 + D(u) \Delta u \sim D'(u_0) \|\nabla \xi\|^2 + D(u_0) \Delta \xi = D(u_0) \Delta \xi + \mathcal{O}(\xi^2)$ and thus the diffusion is the same in all the directions.

thus the activator species, while v refers to the population of inhibitors.

The celebrated Turing patterns originate from a symmetry breaking instability of the homogeneous equilibrium solution. The introduction of an inhomogeneous perturbation around (\hat{u}, \hat{v}) activates the diffusion terms and, under specific conditions, makes the system to drift away from the deputed homogeneous equilibrium, towards a patchy, non homogeneous, asymptotically stable, solution. Mathematical conditions for the Turing instability to set in can be readily derived by first linearizing equations (1) and then Fourier transforming, both in time and space, the obtained linear system. This yields the so called dispersion relation, an equation for the growth rate λ_k associated to Fourier mode $k = (k_x, k_y)$. By carrying out this straightforward calculation, which is for instance detailed in [1], it can be eventually proven that λ_k satisfies the following quadratic equations:

$$\lambda_k^2 + d(k_x, k_y)\lambda_k + h(k_x, k_y) = 0 \quad (6)$$

where:

$$d(k_x, k_y) = -\text{tr}(J) + k_x^2(D_u^{(x)} + D_v^{(x)}) + k_y^2(D_u^{(y)} + D_v^{(y)}) \quad (7)$$

$$h(k_x, k_y) = \det(J) - k_x^2(f_u D_v^{(x)} + g_v D_u^{(x)}) - k_y^2(f_u D_v^{(y)} + g_v D_u^{(y)}) + k_x^2 k_y^2 (D_u^{(x)} D_v^{(y)} + D_u^{(y)} D_v^{(x)}) + k_x^4 D_u^{(x)} D_v^{(x)} + k_y^4 D_u^{(y)} D_v^{(y)}. \quad (8)$$

Turing patterns materialize if the real part of λ_k takes positive values over finite window in k , which in turn amounts to require the presence of unstable non zero Fourier modes. We remark however that $d(k_x, k_y)$ in equation (6) is always positive, since, by assumption, $\text{tr}(J) < 0$ and, in addition, $D_{u,v}^{(x),(y)} > 0$. Then, as a natural consequence, the Turing symmetry breaking instability can take place only if a compact domain exists in (k_x, k_y) such that $h(k_x, k_y) < 0$. As already mentioned, in the classical limit of isotropic diffusion, $D_u \equiv D_u^{(x)} = D_u^{(y)}$ and $D_v \equiv D_v^{(x)} = D_v^{(y)}$, the Turing instability can take place only if the inhibitors diffuse faster than the activators, i.e. $D_v > r_c D_u$ where r_c , the critical ratio of diffusivities, is a positive coefficient larger than 1. In the following we will show that this stringent assumption can be partially relaxed in the generalized setting where the diffusion constants are made to depend on the direction of propagation.

3 Turing instability in presence of anisotropic diffusion

The function $h(k_x, k_y)$ is a multivariate polynomial of the variables k_x^2 and k_y^2 . It is straightforward to check that it is positive at the origin and for large k_x^2 and k_y^2 . We are here interested in determining when $h(k_x, k_y)$ can change sign as function of k_x^2 and k_y^2 , so signaling the onset of the instability. To this end, we first consider restrictions of $h(k_x, k_y)$ on $k_x = 0$, and then on $k_y = 0$.

Focusing on the restriction of h on the k_y axis, i.e. namely setting $k_x = 0$, amounts to consider the particular case where species u and v are solely allowed to diffuse along the vertical direction. One can therefore equivalently set $D_u^{(x)} = D_v^{(x)} = 0$ in equation (8) and thus get:

$$h(k_x, k_y) = \det(J) - k_y^2(f_u D_v^{(y)} + g_v D_u^{(y)}) + k_y^4 D_u^{(y)} D_v^{(y)}. \quad (9)$$

By solving equation (9) for k_y^2 , one obtains two positive solutions, $0 < k_- < k_+$, if and only if the following conditions are met:

$$\begin{cases} f_u D_v^{(y)} + g_v D_u^{(y)} > 0 \\ (f_u D_v^{(y)} + g_v D_u^{(y)})^2 - 4 D_u^{(y)} D_v^{(y)} \det(J) > 0. \end{cases} \quad (10)$$

Let us observe that from the first relation of equation (10) and the condition $\text{tr}(J) < 0$ implies $D_v^{(y)} > D_u^{(y)}$: for the instability to set in and the patterns to develop, the inhibitor should diffuse faster than the activator in the y direction.

The symmetric limiting case is recovered when species u and v are allowed to diffuse only along the horizontal direction, which in turn amounts to restrict h to the k_x axis. The analysis can be hence handled by setting $D_u^{(y)} = D_v^{(y)} = 0$ in equation (8) and proceeding in analogy with above. One can straightforwardly obtain the following necessary and sufficient conditions for the existence of Turing patterns:

$$\begin{cases} f_u D_v^{(x)} + g_v D_u^{(x)} > 0 \\ (f_u D_v^{(x)} + g_v D_u^{(x)})^2 - 4 D_u^{(x)} D_v^{(x)} \det(J) > 0. \end{cases} \quad (11)$$

Once again, from the first relation of equation (11) and the condition $\text{tr}(J) < 0$, one can immediately conclude that patterns are possible only if $D_v^{(x)} > D_u^{(x)}$, namely if the inhibitor diffuses faster than the activator along the x direction.

These conclusions are clearly not surprising, as they constitute an obvious adaptation of the standard Turing framework to the present context, in the trivial limit where one of the diffusion direction is alternatively silenced. Starting from this observation, it is however interesting to speculate on the possibility of turning unstable complex mixed modes (k_x, k_y) , via a symmetry breaking process of the Turing type, when the simplified pathways to pattern formation explored above are instead precluded.

To this end, we go back to function $h(k_x, k_y)$ and study its sign when moving on (k_x, k_y) , along specific directions. More concretely, we set $k_x = \gamma k_y$, and vary the free parameter γ to span the reference plane. Turing patterns can then develop only if $h(\gamma k_y, k_y) < 0$, where:

$$\begin{aligned} h(\gamma k_y, k_y) &= \det(J) - k_y^2[\gamma^2(f_u D_v^{(x)} + g_v D_u^{(x)}) + (f_u D_v^{(y)} + g_v D_u^{(y)})] + k_y^4[\gamma^2(D_u^{(x)} D_v^{(y)} + D_u^{(y)} D_v^{(x)}) + \gamma^4 D_u^{(x)} D_v^{(x)} + D_u^{(y)} D_v^{(y)}] \\ &=: B_1 k_y^4 - B_2 k_y^2 + B_3 \end{aligned} \quad (12)$$

and the last expression defines the coefficients B_1 , B_2 and B_3 . It can be readily realized that B_1 and B_3 are positively definite, while B_2 can assume both positive and negative values. In the following, we shall impose the simultaneous violation of conditions (10) and (11), via crossed negation of the corresponding inequalities, and look for possible values of the control parameter γ that make the system unstable.

3.1 Conditions (10)i and (11)i are not satisfied

Let us thus assume

$$\begin{cases} f_u D_v^{(y)} + g_v D_u^{(y)} < 0 \\ f_u D_v^{(x)} + g_v D_u^{(x)} < 0 \end{cases}$$

while the remaining two conditions (10)ii and (11)ii do hold.

One can trivially realize that in this case B_2 is negative, hence $h(\gamma k_y, k_y) = B_1 k_y^4 + |B_2| k_y^2 + B_3 > 0$ for all $k_x = \gamma k_y$ and k_y . No instability can thus develop which seeds the emergence of self-organized Turing patterns.

3.2 Conditions (10)i and (11)ii are not satisfied

We now assume

$$\begin{cases} f_u D_v^{(y)} + g_v D_u^{(y)} < 0 \\ (f_u D_v^{(x)} + g_v D_u^{(x)})^2 - 4 D_u^{(x)} D_v^{(x)} \det(J) < 0 \end{cases}$$

while the remaining two relations (10)ii and (11)i are verified.

Solving for the limiting condition $h(\gamma k_y, k_y) = 0$ one gets a closed expression for k_y^2 . By imposing k_y^2 to be positive yields $B_2 > 0$ and $B_2^2 - 4B_1B_3 > 0$.

A straightforward computation gives:

$$B_2 > 0 \quad \text{if } \gamma^2 > q_1,$$

where

$$q_1 = -\frac{f_u D_v^{(y)} + g_v D_u^{(y)}}{f_u D_v^{(x)} + g_v D_u^{(x)}} > 0,$$

where use has been made of equation (11)i.

A somehow lengthy computation allows us to write:

$$B_2^2 - 4B_1B_3 = A_1\gamma^4 + A_2\gamma^2 + A_3 \quad (13)$$

where:

$$A_1 = \Gamma_1 - 4 \det(J) D_u^{(x)} D_v^{(x)} \quad (14)$$

$$A_2 = 2(f_u D_v^{(x)} + g_v D_u^{(x)})(f_u D_v^{(y)} + g_v D_u^{(y)}) - 4 \det(J)(D_u^{(y)} D_v^{(x)} + D_u^{(x)} D_v^{(y)}) \quad (15)$$

$$A_3 = \Gamma_2 - 4 \det(J) D_u^{(y)} D_v^{(y)} \quad (16)$$

and

$$\Gamma_1 = (f_u D_v^{(x)} + g_v D_u^{(x)})^2 \quad \text{and} \quad \Gamma_2 = (f_u D_v^{(y)} + g_v D_u^{(y)})^2. \quad (17)$$

Under the above assumptions $\Gamma_1 < 4 \det(J) D_u^{(x)} D_v^{(x)}$, which implies $A_1 < 0$. Similarly, as $\Gamma_2 > 4 \det(J) D_u^{(y)} D_v^{(y)}$, $A_3 > 0$. On the other hand, $A_2 < 0$, this latter quantity resulting from the sum of two negative terms. Hence, $B_2^2 - 4B_1B_3 > 0$ if $0 < \gamma^2 < q_2$, where $q_2 = \frac{A_2 + \sqrt{A_2^2 - 4A_1A_3}}{-2A_1} > 0$.

We can easily show that $q_1 > q_2$, which in turn implies that B_2 and $B_2^2 - 4B_1B_3$ cannot be at the same time positive, as it should happen for the instability to develop. We can hence conclude that Turing patterns cannot develop in this case either.

3.3 Conditions (10)ii and (11)i are not satisfied

Let us thus assume

$$\begin{cases} (f_u D_v^{(y)} + g_v D_u^{(y)})^2 - 4 D_u^{(y)} D_v^{(y)} \det(J) < 0 \\ f_u D_v^{(x)} + g_v D_u^{(x)} < 0 \end{cases}$$

while the remaining two condition (10)i and (11)ii are verified.

Once again requiring $h(\gamma k_y, k_y) < 0$, necessarily imply $B_2 > 0$ and $B_2^2 - 4B_1B_3 > 0$. The former condition is satisfied whenever:

$$\gamma^2 \in (0, q_1)$$

for $q_1 = -(f_u D_v^{(y)} + g_v D_u^{(y)}) / (f_u D_v^{(x)} + g_v D_u^{(x)}) > 0$. The latter condition $B_2^2 - 4B_1B_3 > 0$ yields

$$\begin{aligned} & \gamma^4 (\Gamma_1 - 4 \det(J) D_u^{(x)} D_v^{(x)}) + \gamma^2 [2(f_u D_v^{(x)} + g_v D_u^{(x)})(f_u D_v^{(y)} + g_v D_u^{(y)}) - 4 \det(J)(D_u^{(y)} D_v^{(x)} + D_u^{(x)} D_v^{(y)})] + \Gamma_2 \\ & - 4 \det(J) D_u^{(y)} D_v^{(y)} := \gamma^4 A_1 + \gamma^2 A_2 + A_3 > 0. \end{aligned}$$

Here, $A_1 > 0$ while $A_2 < 0$ and $A_3 < 0$. Hence, the previous inequality is satisfied for any $\gamma^2 > q_2$ for $q_2 = (-A_2 + \sqrt{A_2^2 - 4A_1A_3}) / (2A_1) > 0$. However, one can prove that $q_1 < q_2$, which implies that B_2 and $B_2^2 - 4B_1B_3$ cannot be simultaneously positive. The conclusion is therefore that $h(\gamma k_y, k_y) > 0$, and Turing patterns cannot take place.

3.4 Conditions (10)ii and (11)ii are not satisfied

Let us thus assume

$$\begin{cases} (f_u D_v^{(y)} + g_v D_u^{(y)})^2 - 4 D_u^{(y)} D_v^{(y)} \det(J) < 0 \\ (f_u D_v^{(x)} + g_v D_u^{(x)})^2 - 4 D_u^{(x)} D_v^{(x)} \det(J) < 0 \end{cases}$$

while the remaining two assumptions (10)i and (11)i do hold.

Under the present working hypothesis, the coefficient B_1 , B_2 and B_3 are positive. Thus $h(\gamma k_y, k_y)$ can take negative values, if and only if $B_2^2 - 4B_1B_3 > 0$. As previously remarked, we can rewrite

$$B_2^2 - 4B_1B_3 = A_1\gamma^4 + A_2\gamma^2 + A_3$$

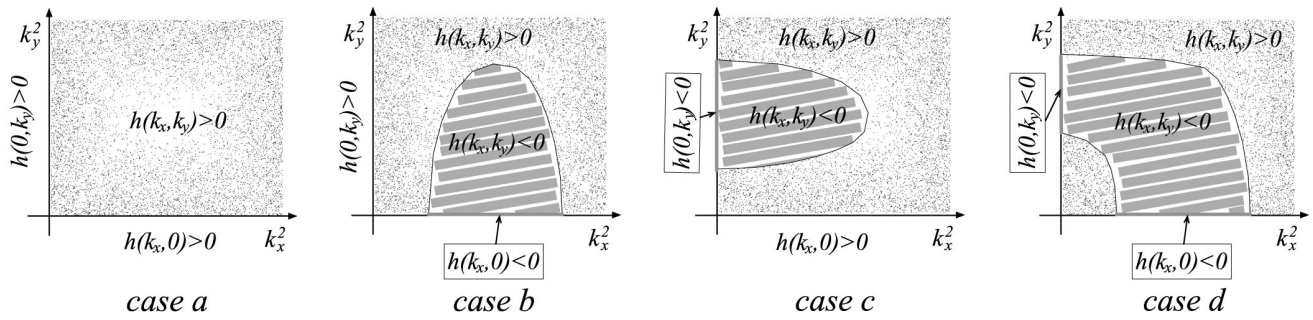


Fig. 1. Possible types of instabilities. Case a: $h(k_x, k_y) > 0$ for all $k_x^2 \geq 0$ and $k_y^2 \geq 0$. The system cannot turn unstable. Case b: h restricted to the k_x axis takes negative values: a bounded contiguous domain in $k_x^2 > 0$ and $k_y^2 = 0$ exist, for which $h(k_x, k_y) < 0$. Case c: h restricted to the k_y axis takes negative values. Again a portion of the reference plan, adjacent to the domain of instability in $k_x = 0$, can be found where $h(k_x, k_y) < 0$. Case d: the system is unstable along both $k_x = 0$ and $k_y = 0$ directions. The instability also interests non trivial modes with both $k_x \neq 0$ and $k_y \neq 0$.

where A_i for $i = 1, 2, 3$ are defined as in (14). One can show that A_1 and A_3 are negative while A_2 can take both signs. To satisfy the requirement $B_2^2 - 4B_1B_3 > 0$ the conditions $A_2 > 0$ and $A_2^2 - 4A_1A_3 > 0$ should be simultaneously met.

Let us rewrite A_2 as follows

$$A_2 = 2\sqrt{\Gamma_1}\sqrt{\Gamma_2} - 4\det(J) \left(D_u^{(y)} D_v^{(x)} + D_u^{(x)} D_v^{(y)} \right)$$

where Γ_i have been defined in equation (17). Straightforward manipulations allow us to write:

$$\begin{aligned} A_2 &= 2\sqrt{\Gamma_1}\sqrt{\Gamma_2} - 4\det(J) \\ &\quad \times \left(D_u^{(y)} D_v^{(y)} \frac{D_v^{(x)}}{D_v^{(y)}} + D_u^{(x)} D_v^{(x)} \frac{D_v^{(y)}}{D_v^{(x)}} \right) \\ &< 2\sqrt{\Gamma_1}\sqrt{\Gamma_2} - \left(\Gamma_2 \frac{D_v^{(x)}}{D_v^{(y)}} + \Gamma_1 \frac{D_v^{(y)}}{D_v^{(x)}} \right) \\ &= - \left(\sqrt{\frac{D_v^{(y)}}{D_v^{(x)}}} \Gamma_1 - \sqrt{\frac{D_v^{(x)}}{D_v^{(y)}}} \Gamma_2 \right)^2 < 0. \end{aligned}$$

Since A_2 is bound to be negative, the condition for Turing instability $h(\gamma k_x, k_y) < 0$ cannot be satisfied.

Summing up we have demonstrated that patterns can eventually develop only if the system can undergo a symmetry breaking instability of the Turing type, in its restricted configuration where the diffusion is solely allowed along one spatial direction, either x or y . The result is summarized in Figure 1, where different types of instabilities are schematically depicted.

Interestingly, the instability can set in also if the inhibitor diffuses slower than the activator along one selected direction, provided the opposite holds for the transport along the orthogonal direction. In this respect, accounting for anisotropic diffusion enables one to partially relax the stringent conditions that underlie the formation of the Turing motifs. In the next section, we will build on this observation and provide a numerical demonstration of the investigated phenomenon.

4 Numerical analysis

The aim of this section is to discuss a numerical implementation of the theory presented above. In particular, we will show that complex patterns can emerge for a system of two species in mutual interaction and undergoing anisotropic diffusion, also if the conventional Turing request of having inhibitors faster than activators is relaxed, along one of the two orthogonal directions of movements. To perform the analysis we operate in the framework of the so called Mimura-Murray model [37]. The quantities u and v can be associated to prey and predator densities, which interact via the nonlinear functions:

$$\begin{aligned} f(u, v) &= ((a + bu - u^2)/c - v)u \text{ and} \\ g(u, v) &= (u - (1 + dv))v; \end{aligned} \quad (18)$$

the model possesses 6 equilibria, whose stability and positivity depend on the value of the chosen parameters. We here focus on the fixed point (\hat{u}, \hat{v})

$$\hat{u} = 1 + \frac{bd - 2d - c + \sqrt{\Delta}}{2d}$$

and

$$\hat{v} = \frac{bd - 2d - c + \sqrt{\Delta}}{2d^2}$$

where

$$\Delta = (bd - 2d - c)^2 + 4d^2(a + b - 1) \quad (19)$$

and assume $a = 35$, $b = 16$, $c = 9$ and $d = 0.4$ which in turn implies $(\hat{u}, \hat{v}) = (5, 10)$. Moreover, the Jacobian entries evaluated at the fixed point reads $f_u = 3.33$, $f_v = -5$, $g_u = 10$ and $g_v = -4$. Hence, $\det(J) > 0$ and $\text{tr}(J) < 0$: the fixed point is a stable equilibrium. We also remark that u acts as the activator and v stands for the inhibitor species, as $f_u > 0$ and $g_v < 0$. Under specific conditions, the fixed point can be destabilized by an external, non homogeneous, perturbation, paving the way to the subsequent generation of Turing patterns, in the non linear regime of the evolution. In Figure 2 we report a gallery

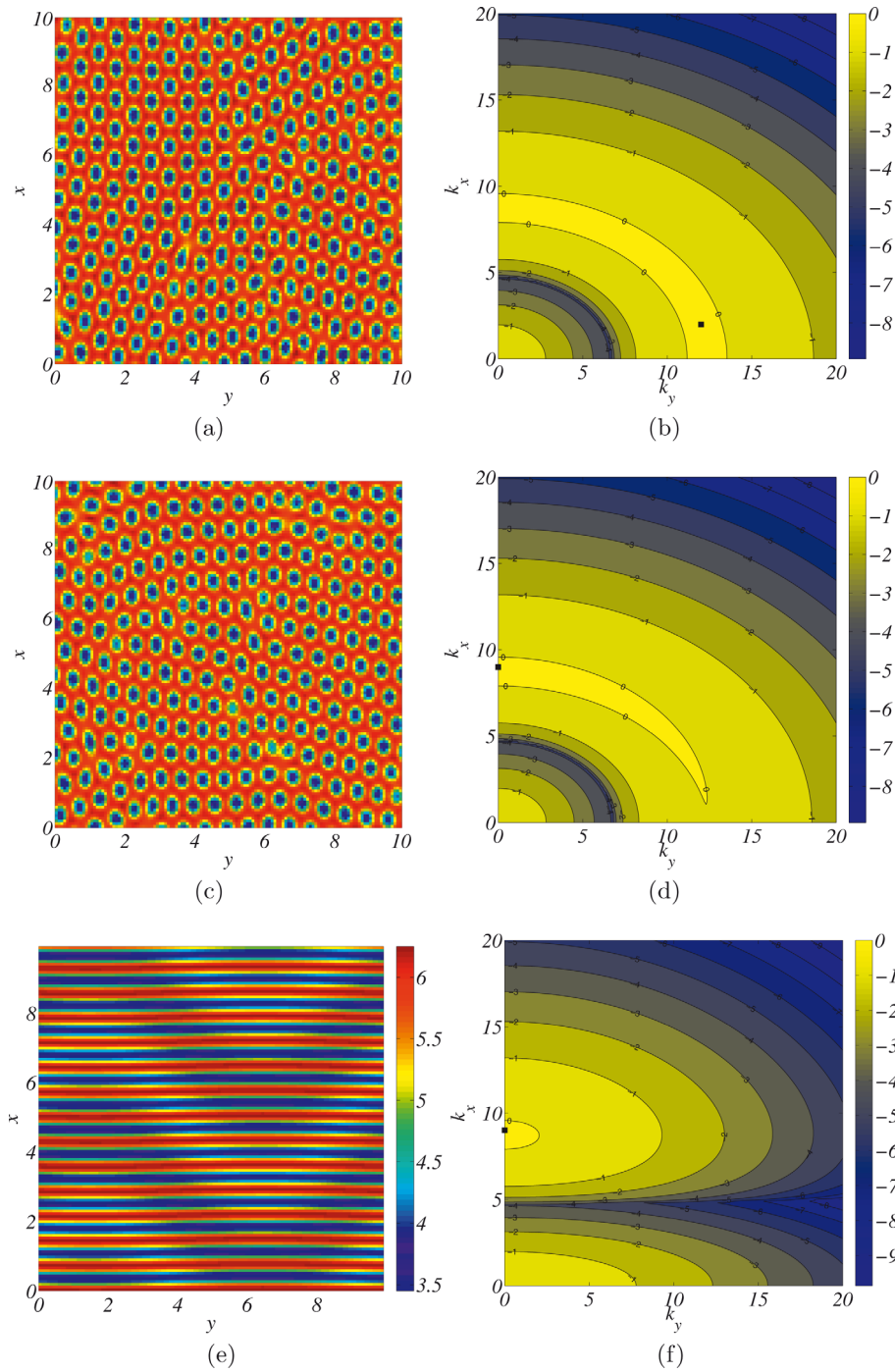


Fig. 2. Asymptotic activator distribution: the concentration $u(x,y,t)$ is displayed for sufficiently large t . (a) $D_u^{(y)} = 0.01$, $D_v^{(y)} = 0.16$, $D_u^{(x)} = 0.02$, $D_v^{(x)} = 0.32$. (b) $D_u^{(y)} = 0.01$, $D_v^{(y)} = 0.155$, $D_u^{(x)} = 0.02$, $D_v^{(x)} = 0.32$. (c) $D_u^{(y)} = 0.012$, $D_v^{(y)} = 0.01$, $D_u^{(x)} = 0.02$, $D_v^{(x)} = 0.32$. The other parameters are set to $a = 35$; $b = 16$; $c = 9$; $d = 0.4$. The filled black squares identify the position of the maximum of the dispersion relation.

of representative patterns that can be obtained under distinct conditions.

To generate the asymptotic patterns displayed in Figure 2a, parameters are set so that both relations (10) and (11) are satisfied, $D_v^{(x)} > D_u^{(x)} r_c$ and $D_v^{(y)} > D_u^{(y)} r_c$, where $r_c \sim 16$. Inhibitor diffuses faster than activators in both x and y directions, although with different diffu-

sion constants. The dispersion relation (see Fig. 2b) can be assimilated to that sketched in Figure 1d, and the corresponding patterns share marked similarities with those obtained in the conventional case of isotropic transport.

In Figure 2c, conditions (10) hold, while (11) do not, $D_v^{(x)} > D_u^{(x)} r_c$ while $D_v^{(y)} < D_u^{(y)} r_c$, where $r_c \sim 16$. The dispersion relation, Figure 2d, is also depicted and shown

to resemble that displayed in Figure 1c. The patterns which follow this unusual choice of the diffusion constants, compare nicely with those emerging under the standard paradigm, this is because $D_v^{(y)}/D_u^{(x)}$ is smaller but close to r_c .

Finally, in Figures 2e and 2f, the activator is assigned a diffusion coefficient $D_u^{(y)}$ is larger than $D_v^{(y)}$, the homologous constant associated to the inhibitor species, and still $D_v^{(x)} > D_u^{(x)} r_c$. The dispersion relation falls in the category exemplified in Figure 1c, and the corresponding patterns are found to organize in regular stripes, which run almost parallel to the direction where the instability is present.

5 Conclusions

In this paper we elaborated on the impact of anisotropic diffusion for the emergence of Turing patterns in reaction-diffusion systems. We have in particular focused on systems of two interacting species confined in a rectangular, continuum domain, endowed with periodic boundary conditions. With reference to this paradigmatic case study, we have analytically shown that a symmetry breaking instability of the Turing type can occur only if patterns do exist when diffusion is impeded along one of the two accessible directions. In other words, patterns which resemble those obtained in the conventional setting of isotropic diffusion emerge, also when the standard Turing condition is violated along one specific direction. Interestingly, the instability can also occur if the activator diffuses faster than the inhibitor, along the direction of spatial relocation for which the usual Turing conditions are not met. Our results complement thus the large literature devoted to patterns formation in reaction-diffusion systems, by elaborating on the role played by a specific class of anisotropic transport.

Author contribution statement

All the authors designed, carried out the study and wrote the manuscript text. T.C. and D.C. prepared the figures. All authors reviewed and approved the manuscript.

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References

1. J.D. Murray, *Mathematical Biology II: Spatial Models and Biomedical Applications* (Springer-Verlag, 2003)
2. A. Ord, B.E. Hobbs, *Phil. Trans. R. Soc. A* **368**, 95 (2010)
3. B.P. Belousov, *Collection of Abstracts on Radiation Medicine* **145**, 147 (1957)
4. S. Strogatz, *Non linear dynamics and chaos: with applications to Physics, Biology, Chemistry and Engineering* (Perseus Book Group, 2001)
5. L. Yang, M. Dolnik, A.M. Zhabotinsky, E.R. Epstein, *J. Chem. Phys.* **117**, 7259 (2002)
6. R. deForest, A. Belmonte, *Phys. Rev. E* **87**, 062138 (2013)
7. M.A. Novak, R.M. May, *Nature* **359**, 827 (1992)
8. M.A. Novak, S. Bonhoeffer, R.M. May, *Int. J. Bifurc. Chaos* **4**, 33 (1993)
9. J.Y. Wakano, Ch. Hauert, *J. Theor. Biol.* **268**, 30 (2011)
10. A.M. Turing, *Phil. Trans. R. Soc. London Ser. B* **237**, 37 (1952)
11. R.A. Satnoianu, M. Menzinger, P.K. Maini, *Math. Biol.* **41**, 493 (2000)
12. B. Ermentrout, M. Lewis, *Bull. Math. Biol.* **59**, 533 (1997)
13. M. Asllani, F. Di Patti, D. Fanelli, *Phys. Rev. E* **86**, 046105 (2012)
14. M. Asllani, T. Biancalani, D. Fanelli, A.J. McKane, *Eur. Phys. J. B* **86**, 476 (2013)
15. T. Biancalani, F. Di Patti, D. Fanelli, *Phys. Rev. E* **81**, 046215 (2010)
16. L. Cantini, C. Cianci, D. Fanelli, E. Massi, L. Barletti, M. Asllani, *J. Math. Biol.* **69**, 1585 (2014)
17. C. Varea, J.L. Aragón, R.A. Barrio, *Phys. Rev. E* **60**, 4588 (1999)
18. D. del-Castillo-Negrete, B.A. Carreras, V. Lynch, *Physica D* **168-169**, 45 (2002)
19. G. Mulone, S. Rionero, W. Wang, *Nonlin. Anal.* **74**, 4831 (2011)
20. A.E. Tikhomirova, V.A. Volpert, *Appl. Math. Lett.* **20**, 163 (2007)
21. M.A. Tsyganov, J. Brindley, A.V. Holden, V.N. Biktashev, *Phys. Rev. Lett.* **91**, 218102 (2003)
22. V.K. Vanag, I.R. Epstein, *Phys. Chem. Chem. Phys.* **11**, 897 (2009)
23. T.C. Lacalli, D.A. Wilkinson, L.G. Harrison, *Development* **103**, 105 (1988)
24. H. Shoji, Y. Iwasa, A. Mochizuki, S. Kondo, *J. Theor. Biol.* **214**, 549 (2002)
25. D. Fanelli, A. McKane, *Phys. Rev. E* **82**, 021113 (2010)
26. D. Fanelli, C. Cianci, F. Di Patti, *Eur. Phys. J. B* **86**, 142 (2013)
27. G. Gambino, M.C. Lombardo, M. Sammartino, *Math. Comput. Simul.* **82**, 1112 (2012)
28. S. Kovács, *Nonlin. Anal.* **59**, 567 (2004)
29. N. Kumar, W. Horsthemke, *Phys. Rev. E* **83**, 036105 (2011)
30. R. Ruiz-Baier, C. Tian, *Nonlin. Anal.* **14**, 601 (2013)
31. E.P. Zemskov, V.K. Vanag, I.R. Epstein, *Phys. Rev. E* **84**, 036216 (2011)
32. E.P. Zemskov, K. Kassner, M.J.B. Hauser, W. Horsthemke, *Phys. Rev. E* **87**, 032906 (2013)
33. S.P. Dawson, A. Lawniczak, R. Kapral, *J. Chem. Phys.* **100**, 5211 (1994)
34. A.B. Rovinsky, M. Menzinger, *Phys. Rev. Lett.* **69**, 1193 (1992)
35. D.A. Vasquez, J.W. Wilder, B.F. Edwards, *Phys. Rev. Lett.* **71**, 1538 (1993)
36. F. Mertens et al., *Phys. Rev. E* **51**, R5193 (1995)
37. M. Mimura, J.D. Murray, *J. Theor. Biol.* **75**, 249 (1978)